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THE LIFE CYCLE OF PARAMECIUM WHEN SUBJECTED TO A VARIED ENVIRONMENT

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STUDIES on the life cycle of *Paramecium aurelia* (*caudatum*) have been made by several investigators, the most extensive work being that of Calkins.¹ As is well known, his results showed that when *Paramecium* was bred continually in a culture medium of hay infusion, it passed through more or less regular cyclical variations in general vitality as measured by the division-rate. The marked periodical depression periods occurred at about six-month intervals and unless the organisms were "stimulated" at this time the culture died out. Minor depressions occurred about every three months, but from these recovery was autonomous. Joukowsky² and Simpson,³ however, apparently found that certain cultures of this organism died out after being but a short time under culture conditions.

A constant culture medium is an important condition for the study of the consecutive phases of vitality, and of the effect of stimuli on the organism, but it is of interest, however, in the light of the results obtained by this method to determine the character of the life cycle of *Paramecium* when subjected to a varied environment. It is possible, of course, that some element is lacking in

¹ Calkins, G. N. Studies on the Life History of Protozoa. I, The Life Cycle of *Paramecium caudatum*. *Archiv f. Entw.*, XV, 1, 1902. IV, Death of the A Series. *Journal Exper. Zool.*, I, 3, 1904.

² Joukowsky, D. Beiträge zur Frage nach den Bedingungen der Vermehrung und des Eintrittes der Konjugation bei den Ciliaten. *Verh. Nat. Med. Ver. Heidelberg*, XXVI, 1898.

³ Simpson, J. Y. Observations on Binary Fission in the Life History of Ciliata. *Proc. Royal Society Edinb.*, XXIII, 1901.

a constant culture medium of hay infusion which is essential to the continued life of the organism, and that depression effects which appear more or less regularly are due, in part, to a process of slow starvation—rather than to a loss of the power of assimilation. Recovery from these periods is effected by various stimuli (beef extract, etc.), because the lacking factor, or factors, is thereby supplied. Calkins himself points out the marked similarity of the morphological changes which he obtained in the earlier cycles of his *Paramecium* cultures with those found by Wallengren⁴ to occur in *Paramecia* which had been intentionally starved. I have also called attention to this similarity in discussing the life cycle of various hypotrichous infusoria and have suggested that the effect of such stimuli as beef extract, etc., may be essentially that of concentrated nutrition.⁵

In connection with some experiments on the effect of various stimuli on the life cycle of infusoria,⁶ I have had occasion to carry a culture of *Paramecium* for over a year, and the data derived from this work are believed to throw some light on the effect of a varied environment on the life history of this organism.

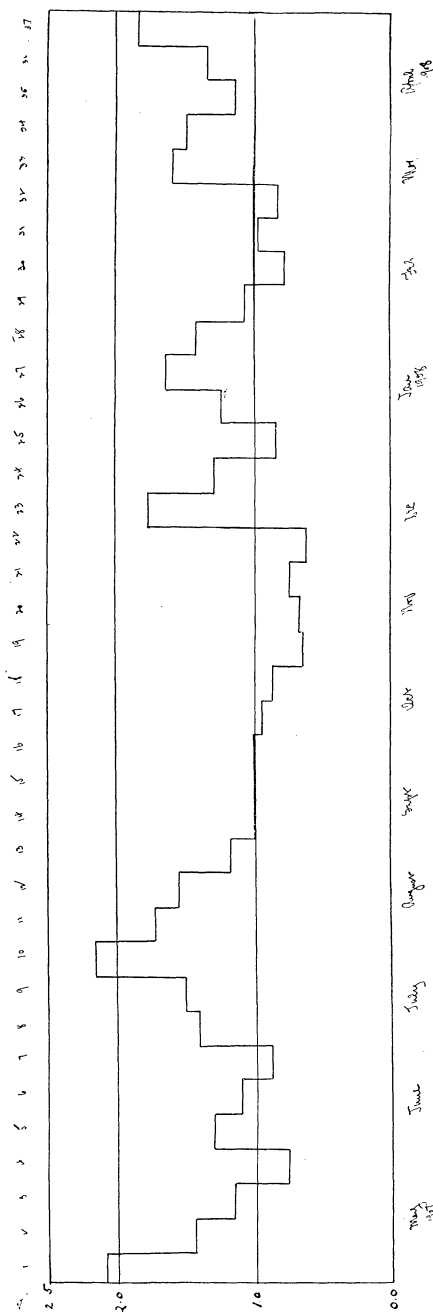
On May 1, 1907, a "wild" *Paramecium* was isolated from a laboratory aquarium and placed on a depression slide in five drops of hay infusion. When this animal had divided twice, the four resulting individuals were isolated on separate slides, and in this manner were started the four lines, I-a, I-b, I-c and I-d, which compose this culture.⁷ The culture has been continued by the isolation of an individual from each of these lines almost daily throughout the life of the culture up to the present time (May 6, 1908) and a record has been kept of the

⁴ Wallengren, H. Inanitionsercheinungen der Zelle. *Zeit. f. allg. Physiologie*, I, 1, 1901.

⁵ Woodruff, L. L. An Experimental Study on the Life History of Hypotrichous Infusoria. *Journal Exper. Zool.*, II, 4, 1905.

⁶ Woodruff, L. L. Effects of Alcohol on the Life Cycle of Infusoria. *Biol. Bull.*, XV, 2, 1908.

⁷ Further details in regard to the technique are given in previous papers.



Complete history of *Paramecium aurelia* (*caudatum*). Culture I, from start on May 1, 1907, to the present time, May 6, 1908, at the 465th generation. The rate of division is averaged for ten-day periods. The ordinates represent the average daily rate of division of the four lines of the culture. Above, the numbers of the ten-day periods are indicated. Below are designated the periods in which the fifteenth day of the respective months fell. The figures, 100, 200, etc., represent generations and are placed in the periods in which they were attained.

daily bipartitions of each line. The following curve represents graphically the average rate of division of the four lines of the culture, and this again averaged for ten-day periods.

The culture was carried on at the Thompson Biological Laboratory of Williams College, Williamstown, Mass., during May and June, 1907; at the Marine Biological Laboratory, Woods Holl, Mass., during July and August, 1907; and at the Sheffield Biological Laboratory of Yale University, New Haven, Conn., from September, 1907, to the present time, May, 1908.

The culture medium during the earlier months of the work consisted of hay or grass infusion. But, except during periods in which the culture was employed as a control for certain experiments, the infusion was made with hay or grass from various localities and different proportions of hay and water were used almost daily. Water from various sources was employed. In every case the temperature of the infusion was raised to the boiling point, and then allowed to attain the temperature of the laboratory before being used. In some cases the infusion was made fresh daily, in other cases it was allowed to stand twenty-four hours before being used.

Beginning in February, 1908, a much more varied culture medium was employed. It was found that *Paramecium* can exist in nearly any infusion which may be made from materials collected in ponds and swamps, and accordingly, in the hope of supplying as far as possible all the elements which may be encountered in the "normal" habitat of the organism, water was taken from ponds, laboratory aquaria, etc., together with its animal and plant life. In other words, no definite method was employed in selecting the material, but it was simply collected at random from many sources, thoroughly boiled, and then used. This culture medium affords a striking contrast to that employed by Calkins, which he described thus, "The hay infusion was made every day, the same amount of hay and water being taken each time and

raised to the boiling point. This method was never varied during the entire period of the cultures and the salt content of the water, as shown by weekly analyses, did not vary beyond a very slight fraction of one part to one hundred thousand."

The only condition present in the life of this culture which could not be encountered by a wild *Paramecium* was the boiled condition of the culture medium, but this was essential in the experiments in order to prevent the introduction of an encysted or active wild individual into the culture.

The objection might be made that the environment was changed too frequently and too greatly to afford natural conditions. But, if the hundreds of millions of wild individuals which are derived from a single wild *Paramecium* are considered, and if the environment of any four lines of descent of four individuals existing at the end of twelve months in the wild state is taken into account, it will be readily appreciated that the surviving organisms have probably experienced far more changes of medium than have the four lines of the culture under consideration. It may be that only those individuals which have encountered varied conditions have survived without resorting to conjugation.

It is obvious, indeed, that all the variations in environment which may be experienced by a wild *Paramecium* have not been supplied; for in a pond considerable changes of temperature occur during the year, and periods of rest by encystment or lack of food are afforded. It is believed, however, that the conditions under which this culture has been carried approach nearer to those encountered by the majority of wild individuals than has been the case in previous investigations.

A glance at the plotted curve of the life history shows that at no ten-day period during the life of the culture up to the present time has the average rate of division of the culture fallen as low as one division in two days, the nearest approach to this rate being attained at period

twenty-two in December, 1907, when the culture was subjected to a particularly uniform culture medium. The highest rate of division so far attained occurred at period ten in July, 1907. The average rate of division for the entire year is obviously considerably above one division per day, the organisms being in the 465th generation on May 6, 1908. That this is not the maximum rate of division of which the culture is capable is shown by the fact that a culture isolated line by line from the one under consideration and treated daily for six months with alcohol is at the same date in the 505th generation.

The major fluctuations in the division rate which have occurred in the life of this culture are all "rhythms" (using this term in the sense in which I employed it in discussing the life history of *Oxytricha*) and so far no "cycle" has been completed. Calkins in his earlier papers on *Paramecium* believed the cycle to be of three months' duration, agreeing in this regard with certain of the earlier investigators on this form. In his last paper on the subject, however, as has been noted, he interpreted the tri-monthly fluctuations as simply minor changes from which recovery was autonomous and regarded the cycle as the larger semi-annual fluctuations, recovery from which was only brought about by stimuli. I have previously interpreted these trimonthly depressions as rhythms and the results obtained from this culture would seem to show that the semi-annual cycles of Calkins are also merely rhythms—recovery from which was not autonomous under the conditions of a constant environment. This culture shows that the cycle of *Paramecium* under a varied environment may be considerably over a year in duration, since the culture at present shows no sign of waning vitality.

This suggests the much-discussed question as to whether the protozoa are potentially immortal, and the rôle of conjugation in the life history. Up to the present time there has been no tendency among the individuals of this culture to conjugate, although in the "stock" cultures,

comprising individuals left over after the daily isolations, there has been every opportunity for its occurrence. Of course there has been no possibility of conjugation in the four direct lines of the culture on account of the daily isolations. This result agrees with that which I obtained with my cultures of various hypotrichous forms—and I believe it suggests strongly that conjugation must be regarded as a more or less variable phenomenon which occurs in the life history when conditions are adverse for the normal life of the organism, and which is not necessary under the conditions of a varied environment. I believe it is customary to regard conjugation as of far more frequent occurrence than it actually is in the life history of “wild” individuals, because it is brought to the attention in laboratory cultures and “hay infusions” which pass through a series of changes—changes which inevitably bring about conditions unfavorable to the continued reproduction of the organisms, and which are compensated for by conjugation.

No period of marked physiological depression is indicated by the division-rate of this culture during the first year of its life; but well-defined morphological changes have occurred. These cytological variations, chiefly nuclear, demand further study. It is evident, however, that the relation of the rate of division to the so-called “normal” condition of the nuclear apparatus of *Paramecium* is not substantiated by this culture, as profound nuclear changes apparently do not affect the rate of division. I believe from a study of this culture and “wild” cultures in large laboratory aquaria, that various nuclear changes which are not at present recognized occur normally in the life history of *Paramecium*, and that possibly when conjugation between two individuals is prevented, either under the conditions of culture or in the “wild” state, a rearrangement of the nuclear apparatus is resorted to which may be analogous to endogamy, or conjugation of nuclei within the original cell.